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THE BOTANICAL REVIEW

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ROOT-ROTS OF CERTAIN NON-CEREAL CROPS[1]

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INTRODUCTION

In a recent publication Simmonds has outlined some of the trends which have appeared in research on root-rots of cereals (286)[2]. The present paper aims to give the status of root-rots of certain non-cereal crops, though no claim is made for an exhaustive review of such rots.

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[2] Reference numbers are given in the text along with an author's name only when there is more than one citation for the author in the bibliography.

That the bulk of the literature on root-rots is of comparatively recent origin is not to be wondered at, since it was only natural that the early pathologists should have investigated first the more obvious diseases, namely, those attacking the above-ground parts, these parts being more apparent and forcing themselves on the attention of those interested in plant diseases. Accordingly, the diseases due to parasitism below ground, that is, root-rots, were left, for the most part, till a later date. One of the several exceptions in this connection was the root-rot of cotton, when Pammell in 1888 reported that the disease which had been killing cotton in Texas was due to a fungus which invaded and killed the roots, and suggested that it could be controlled by proper rotation of crops. The progress made with cotton root-rot investigations in the next 49 years is shown in one list of 157 papers, of which 140 were published during the past 25 years (292). In checking over 619 citations in six papers on root-rots of cotton (292), tobacco (204), sugar cane (247), strawberry (17) and cereals (104, 286), it was noted that 573 or 92.6% also were dated in the last quarter century.

Though most root-rots are general in distribution and few crops completely escape their attack, certain of them may have rather limited distribution. For instance, the destructive one of cotton caused by *Phymatotrichum omnivorum* is confined to the southwestern United States, especially Texas, and adjoining Mexico. Rhododendron wilt and root-rot caused by *Phytophthora cambivora* and the black root-rot of apple caused by *Xylaria mali* have been reported only from the United States. On the other hand, *Armillaria* root-rot of fruit and forest trees and small fruits, and the root-rots of sugar cane and strawberries are present in practically every country where these crops are grown.

The above-ground symptoms of root-rots consist, for the most part, of wilting, yellowing, stunting and often death of affected plants. However, definite diagnosis cannot be made without recourse to examination of roots. Macroscopic examination permits diagnosis of a few common rots characterized by special symptoms, for example, *Armillaria* and *Clitocybe* mushroom root-rots, especially if sporophores are present; red-stele root-rot of strawberries, because of the colour of the stele; black root-rot of tobacco, on the basis of colour; cotton root-rot, especially if spore mats or sclerotia are present; and *Pythium* root-rots of the water-soaked type. But

it is exceedingly difficult if not impossible, without recourse to microscopic examination and isolation, to diagnose many others, since rotted roots, irrespective of causal organism or organisms, have much the same appearance. This is especially true of complex rots where several fungi may be associated with the disease.

As the following résumé points out, not only are many different crops attacked, but the fungi involved are numerous and varied in character, especially as to degree of parasitism. Some are highly specialized parasites that might be classed as "soil invaders", while others, less specialized, more correctly belong to the category of common "soil inhabitants", using these terms in the sense adopted by Garrett (103). Our knowledge of the interrelationships between the hosts and the fungi involved in producing root-rot on these hosts is in far too many instances scanty and incomplete. This is not surprising when it is realized that roots grow in an inert environment of a most complex physical and chemical nature, inhabited by countless numbers and species of living organisms in a dynamic equilibrium. It is this living environment to which roots are subjected that makes the study of root-rots most difficult and involved, since it becomes necessary to evaluate not only the direct host-parasite relationship but also the many direct and indirect effects that changing environment exerts on the biology of the soil in general and the indirect effects these changes in turn exert on the host-parasite relationship. This is particularly true of the complex root-rots where several parasites are implicated.

ROOT-ROTS OF VARIOUS CROPS

Woody perennials. "Mushroom root-rot", caused by *Armillaria mellea* (Vahl.) Fr., is associated mainly with forest and shade trees (43, 127, 128), fruit trees including citrus, small fruits, and other crops, as, for instance, potato. In Europe *A. mellea* attacks primarily forest and shade trees, while in America it affects principally fruit trees and small fruits, and to a less extent forest and shade trees. In Australia in 1910 (161) and in Washington in 1912 (12) it was the cause of a field rot of potatoes. Thus it is evident that the host range is extensive and the disease practically world-wide.

Another "mushroom fungus" capable of causing root-rot of pear, peach, apple, tung and other trees is *Clitocybe tabescens* (Scop.) Bres., though its general distribution is by no means so extensive

as that of *A. mellea.* This rot was reported first on apple in Oklahoma (339), and it has since been found in Florida on 139 species of plants, including a wide variety of fruit, forest and ornamental trees, shrubs and vines (255).

Both *Armillaria* and *Clitocybe* occur mainly on newly cleared land, infection coming from diseased root particles remaining in the ground after the land is cleared. Although in the absence of sporophores these two root-rots may be difficult to distinguish, since the rhizomorphs of both fungi are rather similar, the mycelial growth characteristics are quite different, the mycelium of *A. mellea* and *A. fuscipes* being generally phosphorescent in the dark, a character absent from many cultures of *C. tabescens* (254). Though Rhoads was unable to obtain infection with pure cultures of *C. tabescens* (254), Plakidas has recently been successful in producing it on pear and tung trees by pure culture inoculation (239).

Poole has reported a "mushroom root-rot" on Lucretia dewberry caused by *Collybia dryophila* Fr.

In Europe a root-rot of fruit trees, especially apple and vine, caused by *Rosellinia necatrix* (Hartig) Berlese, has been prevalent many years, having been first reported in 1883 under the name of *Dematophora necatrix* Hartig (129). Later Berlese transferred this fungus to the genus *Rosellinia.* However, it was not till 1934 that the disease was reported in America as causing serious losses to apple trees in California (301). It was pointed out at that time that this rot may be distinguished from those caused by *A. mellea, C. tabescens* and *Xylaria mali* by the absence of well defined rhizomorphs or stromata and the presence of profuse white cottony mycelium adjacent to affected roots. In 1937 this disease was again reported and its genetic relationship with *R. necatrix* confirmed (124). Another species was reported in California on apple orchards and tentatively identified as *R. aquila* (Fr.) De Not. Fawcett cites *R. pepo* Pat. and *R. bunodes* (B. et Br.) Sacc. as root parasites of citrus trees and cacao (87). *R. necatrix* has been reported recently as causing a root-rot of alfalfa in California (125).

Another white root-rot of apple and other fruit trees first reported in 1902 (327) is caused by *Corticium galactinum* (Fr.) Burt. In 1909 this rot was present in various parts of the Ozark Mountains and was able to spread from oaks to fruit trees when the latter were planted on cleared land (328). More recently it has appeared in

Virginia, Maryland, Tennessee, Delaware and Indiana, and its development is "usually so rapid and complete that the presence of the disease in the roots is manifest only in the top by the sudden death of the whole tree in contrast to the much slower acting root rots, as for instance *X. mali* which may be manifested in the top by weak limbs on the side of the tree above the rotted roots" (55). Dewberry, blackberry, Japanese wineberry, dogwood and sumac have been found infected when growing near affected apple trees.

The black root-rot of apple caused by *Xylaria mali* (Ellis & Ex.) Fromme is confined to the more southern States, Virginia, Kentucky, North Carolina, South Carolina, Tennessee, West Virginia, Illinois and Indiana. According to Thomas, *X. polymorpha* (Pers.) Grev. occurs commonly on apple in New York State, and *X. mali* is unknown there (299). The presence of the stromata of *Xylaria* and their attachment to the main trunk and roots, as well as the characteristic black incrustation on the roots, and the brittle, punky character of the invaded wood are certain diagnostic features of this disease. In 1938 Fromme and Schneiderhan demonstrated that stocks became infected with *X. mali* when exposed to infested soil or diseased roots, and they successfully infected trees with pure cultures of the fungus (93). These studies also indicated no resistance in 45 clones of *Malus* exposed to natural infection or in any one of 12 clonal stocks and 11 seedling stocks inoculated with pure cultures.

In 1936 a root-rot of nursery and orchard apple trees caused by *Sclerotium rolfsii* Sacc. was reported (54, 319).

Species of *Phytophthora* are responsible for root-rots of chestnut, beech, cypress, citrus and pine seedlings. Day (65) found *P. cambivora* (Petri) Buis. to be the cause of ink disease of sweet chestnut (*Castanea sativa*), and also associated with a root-rot of beech. Furthermore, *P. cinnamomi* Rand and *P. syringae* Klebahn were isolated from affected roots of chestnut and beech, respectively. Beech is less susceptible than chestnut. Inoculation studies (66) demonstrated that *Castanea sativa, C. crenata* and beech were all susceptible to *P. cambivora, P. syringae* and *P. cinnamomi.* Regarding a root- and collar-rot of *Pinus resinosa* seedlings caused by a species of *Phytophthora* closely resembling *P. cinnamomi,* inoculations with the fungus produced typical effects (152). In this connection it is interesting to note that though species of *Pestalozzia, Sphaeropsis, Sclerotium* and *Rhizoctonia* were associated with *P.*

cinnamomi, none of them produced the typical root-rot in artificial inoculation, though they were capable of producing resiniferous lesions. In 1940 a destructive root- and crown-rot of *Chamaecyparis* was caused by an apparently new species, *P. lateralis* Milb. (216). Plants inoculated with this fungus died within two to six months and the same fungus was re-isolated. According to Petri (236), the most common forms of root-rot of citrus in Sicily are caused by *P. parasitica* Dastur. and *P. citrophthora* (Sm. & Sm.) Leonian, though several other fungi are also associated. *P. parasitica* is, however, the more prevalent. A wilt and root-rot of young rhododendrons, caused by *P. cambivora,* has been described by White (338) and reported also on *Cinnamomum burmanni* (244), *Persea americana* (314, 315, 316, 329), *Pinus resinosa* (152), *Ananas comosus* (195, 214, 280, 281, 282, 284), *Castanea sativa* (217, 235), *Castanea dentata, C. molissima, C. pumila, C. crenata* and *Quercus prinus* (217), *Erica* sp. (24, 229, 317), *Dicranopteris emarginata* (214), *Juglans* sp. (317), *Picea canadensis* and *Quercus rubra* (61) and *Allium cepa* (281, 282).

Other fungi associated with root-rot of citrus in various countries are *Armillaria mellea* (147, 148), *Sclerotinia libertiana* Fckl. (88), *Rosellinia pepo, R. bunodes* (87) and various species of *Fusarium* (89).

Tobacco. Tobacco is attacked by two root-rots, black root-rot caused by *Thielaviopsis basicola* (Berk.) Ferraris (231, 275) and brown root-rot, the cause of which is not known. Since both rots cause stunting and yellowing, examination of roots is necessary for diagnosis. Black root-rot may cause considerable damage to the crop, especially in cool, wet, alkaline soils. Killebrew in 1884 was possibly the first to note and record that "the plants so affected (black root) do not die but after standing comparatively still for a long time revive late in the season but do not make a good quality of tobacco". This characteristic sequence of attack and "standing still" in the early part of the summer, followed by partial recovery, is common with black root-rot. The fact that *T. basicola* requires cool, moist conditions for best growth explains why more severe damage is caused in cool, wet, backward springs and why affected plants outgrow to a large extent the effect of the attack when the warm, dry conditions of summer prevail. Recently, Rawlings reported on three distinct physiologic races of *T. basicola,*

one of which was strongly pathogenic to tobacco, groundnuts and watermelon, but less so to cotton and *Primula obconica;* another damaged watermelons severely, groundnuts less and failed to attack tobacco; while the third was only weakly parasitic to cotton, groundnuts and watermelon, and unable to infect tobacco or *P. obconica. T. basicola* has also been found associated with root-rots on bean, soybean, red clover, cotton, cyclamen, tomato, flax, peanuts, violets, ginseng, cowpeas, parsnips, poinsettia and lupines. Rawlings states that this fungus has been found on 120 species in 30 families.

Though there has been considerable research on brown root-rot of tobacco since 1915, when it was first reported (155), the cause has still to be ascertained. Various agencies have been suggested, namely, parasitic organisms (204), toxic substances in the soil (15, 71), and nutritional disorders (79). The outstanding characteristic of this disease on which there is general agreement is that previous crops of timothy and corn especially favour it. It is considered that such crop effects may be due to toxic substances (274, 31, 51) or depletion of certain substances required by the plants that follow. Infusions of timothy have produced injurious effects on roots of tobacco (71), suggesting that brown root-rot may be only the expression of injurious effects of preceding crops, and in other investigations on infusions of timothy, red clover and tobacco the nitrogen fractions of different infusions were different (78). Later, Eisenmenger demonstrated that timothy and corn decomposed very slowly, whereas tobacco decomposed very rapidly (79). He was able to divide the plants into two groups, the one group—corn, timothy, *etc.,* unfavourable to precede tobacco—showed a high percentage of total nitrogen, a high percentage of total soluble nitrogen, the highest percentage of protein, a low percentage of amides, a high percentage of ammonia, and the lowest percentage of nitrate nitrogen. The other group—favourable as crops to precede tobacco—showed lower percentages of each of these fractions except nitrates. The nitrates in this group were higher. Eisenmenger suggests that plants containing high lignin, high pentosans, high carbon-nitrogen ratios and a subsequent low tendency to protein decomposition in soil may be suspected of being undesirable for tobacco rotation.

Beaumont has also shown a relationship between brown root-rot and decomposition of organic matter. He found that ammonium

compounds, amino acids and certain amides were toxic to tobacco and caused symptoms very similar to those of brown root-rot. He suggested that the disease is indirectly caused by the unoxidized forms of nitrogen that result from decomposition of organic matter, and considered that the root-rotting is due to high nitrogen concentration in the roots, or a narrowed carbon-nitrogen ratio brought about by the rapid absorption of basic nitrogen which makes the roots very susceptible to decay organisms in the soil. He found root-rot most severe under conditions not favourable to nitrification.

More recently it was suggested that *Sclerotium bataticola* Taub. may be the cause of brown root-rot, and it was shown that the cultural habits of *S. bataticola* are in agreement with the limiting factors as related to root-rot under field conditions (204). The authors also were able to produce a condition very closely resembling brown root-rot by inoculation under greenhouse conditions in the presence of a source of carbohydrate, that is, filter paper. In this connection a temperature of 45° C. for 24 hours or 48° C. for 10 to 12 hours completely destroyed the disease-producing agency, but *Rhizoctonia* (*Sclerotium*) *bataticola* (Taub.) Butler was able to withstand 45° C. more than 48 hours, thus raising a doubt as to *S. bataticola* being the causal agent (157). Johnson has also pointed out that careful microscopical examination of free-hand and paraffin sections "failed to show either frequent or extensive invasion of the affected cells by fungi of any sort", a condition not in keeping with the theory of parasitic attack. He concludes: "the failure to find a microscopically visible organism in or between the diseased cells lends support to the idea that a typical parasite is not involved". At the same time he says: "it does not disprove the possibility that organisms confined largely to the exterior of the roots or harboured only in the soil itself may excrete toxic substances that are necrotically injurious to the roots" (157).

Cotton. In the southwestern United States *Phymatotrichum* root-rot of cotton is widespread and serious. In addition to cotton this fungus attacks some 1700 species of plants (297), a fact which must be taken into consideration from the standpoint of crop rotation and control measures. Because of this fact, as well as the nature of the fungus itself which produces sclerotia in abundance, this rot has been most difficult to control, and has received more attention by research workers than possibly any other root-rot to

date. The pertinent literature, most of which deals with various pathological and agronomical phases of the disease, has recently been reviewed (292, 250). In broad outline these papers have dealt with symptoms, the fungus responsible, rate and manner of spread, influence of environment, host range, varietal susceptibility, reaction of soil and control, including crop rotation, fallow, cultivation, soil amendments, especially with manure, organic materials and fertilizers. More recent papers deal with control and its microbiological aspects (62, 220). *Phymatotrichum* root-rot is of special interest in that it seldom produces stunting or dwarfing, as is the case with many root-rots, but rather causes yellowing and wilting of the leaves, followed rapidly by death in most cases. In addition, this rot may be diagnosed by the presence of spore mats on the surface of the ground around affected plants. These mats, which vary from a few inches to a foot or more in diameter, are white at first but later turn a tan colour. In addition to spore mats this fungus produces sclerotia in abundance, under some conditions, and their presence is helpful for diagnostic purposes. In the Punjab of India both American and indigenous cotton is subject to a root-rot in which *Rhizoctonia solani* and *R. bataticola* are involved. This disease has been studied from many angles, including physical and chemical factors, chemical composition of healthy and diseased plants, temperature and moisture relationships and the effects of intercropping (321–326, 198).

Sugar beets. Several fungi are associated with root-rots of sugar beets. Wherever they are grown, black-root is of considerable importance. In Europe especially this root-rot has caused serious losses and has been the subject of many investigations. Black-root is primarily a seedling disease, and as the disease may be seed-borne, seed treatment is generally recommended. Ceresan has given satisfaction in most cases. Five different fungi are associated with the condition, namely, *Phoma betae* (Oud.) Fr., *Rhizoctonia solani* Kühn, *Pythium debaryanum* Hesse, *Aphanomyces cochlioides* Drech. and *Fusarium* sp. Of these it is generally agreed that *P. betae* is the most important, as regards both distribution and degree of parasitism. Campbell in Washington reports that of 31 different fungi isolated from sugar beets and tested for pathogenicity, only *P. betae* gave positive results. In Germany sugar beets are subject to root-rot or blackleg caused by *P. betae, P.*

debaryanum and *Aphanomyces levis* Edson non DBy, *P. betae* being more common and important (178, 232). In Sweden *P. debaryanum* is important (11).

In addition to being associated with other fungi in causing blackroot of sugar beet seedlings, *R. solani* is also capable of producing a dry rot of sugar beets at all stages of development. A study of 78 isolates of *Rhizoctonia* from sugar beet and potatoes gave evidence in support of the claim that the strains from potato stems or tubers are unable to infect sugar beet, indicating that the sugar beet strains may be distinct pathogenically from those attacking potato (190, 192). On the other hand, there are cases where *Rhizoctonia* root-rot on sugar beet was much more severe when sugar beets or potatoes preceded sugar beets than when sugar beets followed maize or small grains (barley) (37, 206, 207). Buchholtz reported that 50% of the sugar beets on the part of a field previously planted to potatoes became infected with *Rhizoctonia,* while only 1.6% became infected on that part of the same field which had been cropped to barley the previous season. In this connection, though 64 isolates from potato stems or tubers were unable to infect sugar beets, three isolated from potato stolons were capable of causing appreciable decay of sugar-beet roots, while nine isolates produced slight decay and thirteen were non-pathogenic (192). Field surveys in 1936, 1937 and 1938 indicated that where sugar beets followed sugar beets, root-rot was more severe than where sugar beets followed potatoes. In fact, sugar beets following potatoes were relatively free from root-rot. Nevertheless, in Iowa and elsewhere root-rot has been correlated with preceding crops of potatoes, and the fact that certain strains of *R. solani* may attack potatoes, as shown by Le Clerg, would explain such an association. In addition, there is the possibility that other strains of *R. solani,* though unable to parasitize potato stolons or tubers, may under favourable conditions "colonize" as saprophytes on or in close proximity to potato roots and thus be ready to attack sugar beets the following season. Sugar beets, as well as certain other field crops, are subject to attack by another species, *R. crocorum* (P.) ex Fr. (*Helicobasidium purpureum*), known as the violet, red or root killer root-rot.

Leach (183) considers the most important root-rots of sugar beets in California to be southern rot caused by *Sclerotium rolfsii*

Sacc. and dry rot canker caused by *Rhizoctonia solani,* though a wet rot caused by *Phytophthora* sp. is also of some importance. In Utah *Phytophthora drechsleri* Tucker was destructive mainly in the heavier, poorly drained soils (307). In addition to California and Utah, it has been found also in Idaho and Colorado. In 1939 Greis reported that *Macrosporium cladosporioides,* hitherto known only as a saprophyte associated with sugar beets, was in reality a joint agent with *Pythium debaryanum* and *Alternaria tenuis* in causing a typical root-rot of sugar beets in Germany.

Peas, vetches, clovers. Several organisms are recognized as causing root-rot of peas, vetches and sweet clover. *Aphanomyces euteiches* Drech. is of prime importance, with species of *Rhizoctonia* and *Pythium* playing a secondary rôle (74). Another root-rot of peas in Canada is due to *Fusarium vasinfectum* var. *pisi* Atk. and *P. debaryanum* in association (290, 291). *Fusarium* alone produces a browning and *Pythium* a blackening of the tissue, whereas both together produce typical root-rot or blight. Weimer (334) considers that root-rot of peas in southern United States is due primarily to *A. euteiches* with which are associated *P. graminicola* Subr., *P. irregulare* Buis., *Rhizoctonia* sp., *Fusarium* sp. and bacteria. In Tasmania, too, a root-rot of peas is caused by *A. euteiches* (105). Though species of *Fusarium* and *Pythium* were isolated from diseased roots as well as *A. euteiches,* inoculations indicated that neither of these fungi was capable of producing the rot. In New Jersey a root-rot of peas caused by *A. euteiches* also attacked sweet pea, hairy vetch, cowpea and sweet clover (119, 120). *Fusarium coeruleum* (Lib) Sacc. (126), *F. martii* var. *pisi* App. and Wr., *R. solani, Ascochyta pinodella* L. K. Jones and *Mycosphaerella pinodes* (Berk. & Blox.) Stone (331) have also been associated with root-rot of peas.

In Wisconsin (331), the Middle Atlantic (74) and the Southern (334) States, as well as in Tasmania, *A. euteiches* is considered to be the most important organism in the pea root-rot complex. However, in New York State *Fusarium solani* (Mart.) v. *martii* (App. et Wr.) Wr. f. 2 Sny. was the most important organism (252*a*). In a comprehensive study over a ten-year period (1931–41), *F. solani* v. *martii* f. 2 was an active parasite under all conditions investigated, whereas *A. euteiches* was of little consequence under dry conditions (252*a*). The organisms associated with pea root-rot

ranked in the following order of importance: *F. solani* v. *martii* f. 2, *A. euteiches, P. ultimum, R. solani* and *Ascochyta pinodella* (252*a*). Jones has recorded a wilt and root-rot caused by *F. vasinfectum* v. *pisi* as being very destructive in the United States (162). This disease differs from the other typical root-rots in that it is primarily a vascular disease resulting in wilt, though roots are also attacked. Buisman considers that *P. irregulare* is the cause of a root-rot of peas in Holland.

R. solani is also capable of producing a serious root-rot of sweet clover, as reported recently in Manitoba, Canada, and Minnesota. All seedlings in inoculated plots were killed under certain conditions, and *R. solani* was isolated most commonly in the early stages, but species of *Fusarium* predominated in more advanced stages, thus indicating that *R. solani* was primarily responsible (46).

Phytophthora cactorum (Leb. & Conn.) Schroet. was shown in 1940 as the cause of a destructive root-rot of sweet clover in Alberta (59). The same disease had been reported earlier as being caused by *Phytophthora megasperma* Drechs. (163), though the two authors now agree that the fungus responsible for root-rot of sweet clover in the United States is *P. cactorum* and not *P. megasperma. P. cactorum* is also responsible for a black root-rot on hops in New Zealand (32).

Sugar cane, corn, pineapple. Pythium arrhenomanes Drechsler is a strong parasite against the roots of sugar cane in practically every sugar-producing country. Carpenter in Hawaii was the first to establish this. While it is the principal agent in the United States, 12 other species of *Pythium,* including *P. dissotocum* Drech. and *P. graminicolum,* and other fungi are associated with the rot (247). In Coimbatore, a root-rot of sugar cane was caused by *P. debaryanum* (243). *Rhizoctonia solani* and *R. palida* Matz. have also been reported as causal agents, especially in Puerto Rico (205), Barbados (28) and Louisiana (77), but they are not considered so important as *P. arrhenomanes.* In addition to sugar cane, *P. arrhenomanes* and other species of *Pythium* attack the roots of field corn and milo sorghum (80, 154, 258), causing a serious rot under certain field conditions. It was found that in most cases *P. debaryanum* was the first parasite attacking corn roots, followed by *P. graminicola* when the temperature became higher. At the same time *Gibberella saubinettii* (Durieu & Mont.)

Sacc. and *R. solani* became active, and as the season advanced, *Helminthosporium sativum* P.K. & B. and *Fusarium* spp. produced further necrotic lesions, thus suggesting that corn root-rot is of a complex and progressive type (140, 141). From a root-and-stalk-rot complex of sorghum, *Sclerotium bataticola* and species of *Fusarium, Helminthosporium* and *Pythium* (not *arrhenomanes*) were isolated, and inoculation tests indicated that *Pythium* sp. and *S. bataticola* were capable of causing the seedling blight stage of this complex (145). In Ontario members of the genus *Helminthosporium,* and to a lesser degree *P. debaryanum,* were associated with *P. arrhenomanes* as causal factors of root-rot of field corn (258).

In connection with root-rots of pineapple, nine species of *Nematosporangium,* eleven of *Pythium, Pseudopythium phytophthora, Phytophthora meadii* and *P. melongenae* were more or less pathogenic to smooth Cayenne roots in Hawaii (282, 283). Of these, *N. rhizophthoron, N. polyandron, Pythium splendens* and *P. diamesan* produced more severe damage than the others. However, Rands and Dopp (246), after comparing the above nine forms of *Nematosporangium* with *P. arrhenomanes* from corn and sugar cane, concluded that all nine forms should be referred to *P. arrhenomanes.* Sideris has also described a new species, *Rhizidiocystis ananasi,* as a strict parasite of root hairs of pineapple (278). In Queensland, Australia, Lewcock reports a root-rot of pineapple caused by *Phytophthora cinnamomi.* Johnson found that *P. arrhenomanes* (*N. rhizophthoron*) and species of *Fusarium, Verticillium* and *Rhizoctonia* were associated with root-rots of pineapple in Hawaii. He also reports on *Rhizidiocystis ananasi* in this connection.

Flax. In connection with a root-rot of flax, *Pythium megalacanthum* de Bary was parasitic in the absence of *Asterocystis radicis* de Wildeman (40) which had been reported previously as the cause (200). Buisman suggests that "flax-fire" (scorch) or wilt disease of flax is not a simple disease, but that several fungi may be associated with it in addition to *A. radicis* and *P. megalacanthum.* Diddens verified these findings when she demonstrated that *P. megalacanthum* was responsible for flax scorch. She also found that *A. radicis, Thielaviopsis basicola* and various Phycomycetes (probably *Pythium* spp.) were present in diseased roots,

though to a much less extent than was *P. megalacanthum.* In this connection Boyle has shown certain characteristics of varietal resistance of flax to wilt and root-parasitic fungi with which *T. basicola, P. megalacanthum* and *Rhizoctonia* sp. are associated in North Dakota.

Soya beans, broad beans. A root-rot of soya beans caused by *Pythium debaryanum* has been reported in North Carolina (193), and one of broad beans (*Vicia faba*) in Melbourne district, Australia, caused by *Pythium fabae* (45).

Ginseng. In North America ginseng is subject to at least two root troubles, a "rust" and a "disappearing soft rot", with which species of *Ramularia* have been associated (16, 136, 346). Though Hildebrand was able to prove that *R. panacicola* Zins. as well as two new species, *R. mors-panacis* Hildebrand and *R. robusta* Hildebrand, were capable of producing the rot, he was unable to do so respecting the rust form. He suggests, however, that it is probably caused by representatives of *Ramularia,* since members of this genus were commonly isolated from rusted roots. From Korea come reports of two rots, a red rot and an amber-coloured rot, both of bacterial origin (222).

Strawberries, raspberries. Strawberries are subject to two important root-rots, the red core or red stele root-rot, as found in England, Scotland and America, and the black lesion root-rot complex, as found in England, Canada, France, Holland, Australia, Africa and the United States. In 1934 Berkeley (17) summarized the situation as it existed at that time, and pointed out that the decline of strawberries in many countries was hardly to be attributed to any one cause, though root-rots must be considered as one of the factors.

The red stele or Lanarkshire disease, undoubtedly the more serious, was first ascribed to a species of *Phytophthora* though without proof of its pathogenicity (2–4). In 1940 Hickman, working in England, isolated the red stele *Phytophthora,* proved its pathogenicity and named it a new species, *P. Fragariae* (134). The disease was first reported in the United States in Illinois in 1935, and since then has been found in Delaware, New York, New Jersey, Maryland, California, Virginia and Michigan. Its outstanding symptom is the red coloration of the stele in affected roots, whence it derives its name. Oospores of the fungus are generally to be

found in the discolored stele. Another characteristic is the lack of fibrous roots, which has given rise to the term "rat tail roots", so commonly associated with this disease.

The black lesion or black root type of root-rot, though more widespread, is not so destructive as the red stele disease. Though this type of root-rot has been reported in most countries where strawberries are grown, and though the cause has been ascribed to various factors, such as winter injury, spring frosts and unfavourable soil, it is generally agreed that certain parasitic fungi play a leading rôle in its production. However, the unusual feature is that no single fungus is constantly associated with it, but rather several organisms. Moreover, though several of the fungi appear to be constantly associated with black root-rot wherever it is found, there is considerable variation in the "associated groups of fungi". Hence, this is regarded as a root-rot complex. For instance, in England *Coniothyrium Fuckelii* Sacc., *Fusarium orthoceras* App. & Wr., *Cylindrocarpon radicicola* Wr., *Pachybasium candidum* Sacc. and *Hainesia Lythri* (Desm.) v. Höhn were capable of producing the lesion type (20), and previously *C. Fuckelii* and *H. Lythri* were found responsible for it in Michigan (293). In Ontario species of *Pythium, Ramularia, Alternaria, Verticillium, Cylindrocladium, Rhizoctonia* and *Asterocystis,* plasmodiophoraceous fungi and the phycomycetous mycorrhizal fungus which has been found in the roots of many plants, are all associated with the lesion type of root-rot (313). Hildebrand, also working in Ontario, has reported that microscopic examination showed the presence of "endophytic mycorrhizal fungus", two forms of *Rhizoctonia, Asterocystis, Pythium* spp., *Ramularia* and nematodes, thus indicating their association with black root (135). In Utah isolations from black lesion root-rot most commonly gave *Fusarium orthoceras* and species of *Rhizoctonia, Cylindrocarpon, Hainesia* and *Coniothyrium* (257). Inoculations showed *F. orthoceras, R. solani* and *Cylindrocarpon obtusisporium* capable of inducing the rot. *Olpidium brassicae* and the phycomycetous mycorrhizal fungus were also present in the cortical layers of affected roots.

In addition to the above, species of *Fusarium, Rhizoctonia, Actinomyces, Pythium* and *Coniothyrium* and other fungi have been reported in various countries as being associated with a root-rot condition of strawberries. Though *R. solani* was associated with

root-rot of strawberries in Michigan in 1924 (56) and in Kenya in 1926 (208) it remained for Zeller to prove this relationship by inoculation. Confirming evidence has been reported from Southern Rhodesia (146), Canada (135, 313), Florida (35), Tennessee (276), California (300), New Jersey (202), Australia (1) and Louisiana (238).

According to Berkeley (18), raspberries are subject to a root-rot complex similar to that affecting strawberries. He found that *Coniothyrium Fuckelii, Cylindrocarpon radicicola, Fusarium orthoceras* and *Rhizoctonia solani,* species of *Pythium, Cylindrocladium* and *Rhizoctonia* (orchid type), and nematodes were associated with it. These same organisms have been connected with root-rot of strawberries, and Berkeley found both strawberries and raspberries afflicted with the complex in certain fields of British Columbia.

Vegetables. So far as vegetables are concerned there does not appear to be any serious root-rot that is universal in distribution, though several have been reported in various localities.

Howells (150) has investigated a serious one of tomatoes caused by a species of *Phytopthora* which he considers to be different from *P. parasitica* and *P. cryptogea. P. parasitica* has been reported as attacking fruits and stems of tomato as well as seedlings and roots (251, 259) ; *P. cryptogea* as the cause of a foot-rot of tomato (233).

Pink root on onions caused by *Phoma terrestris* Hansen has been reported by several workers (64, 122, 123). Recently Kreutzer (177) has enlarged our knowledge on this disease by pointing out that, in addition to onions, *P. terrestris* may also attack the roots of young plants of soya bean, pea, cane, millet, oats, barley, wheat, corn, squash, cucumber, cantaloupe, muskmelon, tomato, pepper, eggplant, cauliflower, carrot and spinach. In 1940 a pink root disease appeared on tomatoes apparently due to *P. terrestris* (303).

. In 1939 a watery root-rot of cucurbits in Arizona caused by *Pythium aphanidermatum* (Edson) Fitz. also affected honeydew melons, quil muskmelons and crookneck squash, and caused rapid decay in apples, cantaloupes, carrots, cucumbers, eggplants, grapes, summer squash, sweet potatoes and tomato fruits artificially inoculated and maintained in a moist chamber (111). This same species is considered the cause of a root-rot of Coco-yams on the Gold Coast (341).

Recently a root-rot of pepper and pumpkin, caused by *Phytophthora capsici* Leonian, was shown to be also capable of infecting

squash, eggplant and tomato (311). This fungus has been reported also as the cause of root-rot of chillies in Italy (63), of collar-rot of chillies in Macedonia (272), of blighting of aerial parts as well as girdling of pepper plants at soil level in Florida (333), of damping-off of pepper seedlings (176), and of mildew or blight of chilli peppers in the Argentine (110). Trotter in Italy reported a wilting of pepper due to root infection by *P. omnivora* de Bary, and Kreutzer (177) found that *P. terrestris* attacked the roots of seedlings of 19 different crop plants. *P. megasperma* has been reported as the cause of a root-rot of cauliflower in California in waterlogged soils, and artificial infections were obtained only when the soils were waterlogged (308, 309).

A foot-rot of rhubarb caused by *P. parasitica* var. *rhei* (108) and a tuber-rot of potatoes in Florida caused by *Xylaria apiculata* Cooke (265) have also been reported.

Herbaceous ornamentals. Root-rots have been observed on many ornamentals. Berkeley (19) in Ontario found that chrysanthemums, gladioli, roses and tulips were subject to a rot complex similar to that affecting raspberries and strawberries. He states: "It has become increasingly apparent that these root-rots are the result of a complex of factors in which parasitic organisms play a major rôle, and that this complex may vary with changing conditions of environment. For instance, not only the severity, but the type of organisms may change during the season. Greenhouse crops affected with root-rot often apparently outgrow this condition, and microscopic examination of the roots of such plants throughout the season has indicated a changing fungus flora in the roots".

Rhizoctonia solani, associated with three species of *Pythium,* has been reported on viola and pansy in two forms of root-rot, an epidemic form caused by *R. solani* alone, and a slow form with which are associated two or more of the fungi. It is suggested that the less severe is the result of mild antagonism between the organisms (47).

Buisman has reported on *Pythium* spp. causing a root-rot of cuttings. She found *P. intermedium* de Bary and *P. splendens* Braun. strongly parasitic on roots of geranium cuttings, while *P. debaryanum* and *P. splendens* were parasitic on chrysanthemum cuttings. In 1939 a root-rot and wilt of the Persian buttercup

(*Ranunculus asiaticus*) was caused by *P. debaryanum,* and it was demonstrated, by artificial inoculations, that, though not associated with the disease in the field, *P. irregulare* and *P. ultimum* Trow. were both capable of producing symptoms similar to those produced by *P. debaryanum* (306).

A root-rot, shoot-rot and shanking of forced tulips has been attributed to *Phytophthora cryptogea* Pethybr. & Laff. and *P. erythroseptica* Pethybr., either singly or in conjunction (39), and *P. cryptogea* is the cause of a foot-rot and root-rot of China aster, annual stock and Transvaal daisy (310), while *P. Richardiae* is responsible for a root-rot of Calla lilies in Holland (40), England (267) and the United States (304). A root-rot of paeonies (36) is caused by *P. peoniae* Cooper & Porter, and other fungi.

Tompkins, Tucker and Gardner (309), while working with a root-rot of cauliflower in California caused by *Phytophthora megasperma,* demonstrated experimentally that stocks, wallflower and cineraria were susceptible to the same fungus.

TEMPERATURE IN RELATION TO ROOT-ROT

That temperature plays a most important and in many cases a limiting rôle in relation to root-rots is readily seen by reference to the literature. *Pythium* rot of sugar cane was most severe at 65–68° F., and decreased in severity as the temperature was raised (247); in another instance it was more severe at 15° C. than at 30–35° C. and in wet than in dry soil (91).

It has been indicated that *Phymatotrichum omnivorum* (Shear) Duggar is readily checked by low temperatures and low moisture conditions (261, 294). High temperatures (around 80° F.) during the summer months favoured severe infection, but a drop in early November to about 50° F. produced sharp decline in infection in spite of abundant rainfall (294). The optimum temperature appears to be approximately 27° C., and temperatures of 39° C. or above killed the fungus (261).

Though occasional infection with *Aphanomyces euteiches* may take place through practically the entire range of temperatures at which peas will grow, infection is not abundant nor does invasion proceed rapidly below 15° C., the optimum being between 15° and 30° C. (164). Infection does not take place until the soil temperature is 14° C. or higher for a period of several days (120). The

less important pathogen in the pea root-rot complex, *Fusarium martii* var. *pisi,* has a temperature range of 24° to 33° C. (162). In Wisconsin the important temperature range for several of the fungi associated with root-rot of peas were as follows: *Aphanomyces,* 15° to 30° C.; *Pythium* spp., 16° C. or above; *Rhizoctonia,* 9° to 18° C., and *Ascochyta,* 18° to 21° C. These figures clearly indicate, as Jones has pointed out, that root-rot may be initiated early in the season by *Aphanomyces* or *Rhizoctonia* when the soil is cool; then, when the soil warms up, *Fusarium* species may complete the attack started by low temperature fungi. No infection with *Aphanomyces* root-rot of peas was obtained at 12° C. (287), though slight infection was previously secured at 10° C. (164). Harter has reported that *Fusarium coeruleum,* which causes a root-rot of peas, has a temperature range of parasitism between 10° and 40° C. that corresponds fairly closely with the temperature range at which the host will grow.

Temperatures below 15° C. are unfavourable for *Pythium debaryanum* on sugar beets (38), and *R. solani* on the same host was most active between 30° and 35° C. (191). At 15° to 17° C. rate of decay was exceedingly slow.

Bliss, in a study of the relationship of temperature to *A. mellea,* found that severe infection of *Citrus sinensis* and *C. aurantium* (sweet and sour orange) occurred at 10° C., while infection was moderate at 17° C. and slight at 24° C. In *Prunus persica* (Lovell peach), *P. armeniaca* (Royal apricot) and rooted cuttings of *Pelargonium hortatum* (geranium), it was moderate at 10° and severe at 17° and 24° C. At 31° C. the inoculum was not viable and the roots were all healthy.

Johann, Holbert and Dickson (154) report that the "Pythium injury of dent corn depends upon environmental conditions. Germination may be prevented at low temperatures (12–16° C.) particularly in wet soils, by the rapid rotting of the embryo". At 12° C. they obtained a 57.1% loss of plants due to *Pythium arrhenomanes,* while at 16°, 20° and 24°, the loss was only 33.2, 2.1 and 2.2%, respectively, thus clearly indicating that infection by *P. arrhenomanes* is favoured by temperatures around 12° to 16° C.

In connection with root-rots of strawberry Nolan has reported that most damage by a species of *Diplodia* occurs when the temperature is above 80° F., while Hildebrand (137) found that the black

lesion root-rot, as it occurs in Ontario, was favoured by temperatures above 48° F. Moreover, he found that strawberry plants escaped infection at 44° to 48° F. when grown in root-rot soil adjusted to contain 60% of its maximum water-holding content.

That temperature plays an important rôle in connection with black root-rot of tobacco is well established, since in a heavily infected soil little disease is found if soil temperature is below 15° C. or above 26° C. The most favourable temperature range is between 17° and 23° C. (158), though Doran (72) has pointed out that soil reaction influences the effects of temperature. In connection with brown root-rot of tobacco, Johnson (157) writes that the causal agent is destroyed in 24 hours at 45° C.

Though it is apparent that temperature has a direct effect on root-rots caused by strong parasitic fungi, and that such effects are primarily on the fungi rather than on the host, its rôle in complex rots of the strawberry type is not so apparent, largely because several fungi are involved. In such cases a temperature that favours one group may adversely affect other groups, and, therefore, temperature may be responsible in part at least for the various sequences encountered in such rots. Moreover, in this type the indirect effect of temperature on the general soil flora may play an important rôle in favouring one group at the expense of another, especially if the temperature is such that toxin producers are favoured and certain antagonistic capabilities are enhanced.

REACTION OF THE SOIL

The influence of soil reaction in connection with certain root-rots is well established. For instance, *Thielaviopsis* of tobacco and *Phymatotrichum* of cotton are reduced by increasing soil acidity (70–73, 221). Doran's studies on the effect of temperature and reaction on black root-rot show clearly the influence of soil reaction on infection at different temperatures. For instance, he found when the reaction was pH 5.6 or lower, there was no rot or only a trace at any temperature. Marked injury began at pH 5.7 at 15° C., at pH 5.7 or 5.8 at 18° C., at pH 5.8 at 21° and 24° C., and at pH 5.8 or 5.9 at 27° C. There was little or no injury at 30° C., even in soil with pH values of 6.0 to 6.9. Anderson also found that black root-rot was severe in soils with a pH value of 5.9 or higher, but was unimportant in soils with pH 5.6 or lower (6–8).

He concluded that no injury occurs below pH 5.6 but that between pH 5.6 and 6.0 there is a doubtful zone within which the rot may or may not occur (7). The critical point appears to be at pH 5.9. Others have shown that though *Phymatotrichum* grows best in culture at about pH 7.0, nevertheless, the root-rot of cotton for which it is responsible is found in soils of pH 5.5 to 6.4 as well as in neutral soils of pH 6.5 to 7.4 and alkaline soils of pH 7.5 to 9.0 (295). However, the percentage of diseased fields was twice as high and rot was much more destructive where the soil was alkaline or neutral, than where it was acid. On the other hand, they found *Fusarium* wilt much more common on the acid soils. Little or no growth of *P. omnivorum* was reported in a synthetic nutrient solution when the source of nitrogen was $(NH_4)_2SO_4$ (227, 83). Use of ammonium compounds for treatment of perennials infected with *Phymatotrichum* root-rot has been recommended, since $(NH_4)_2SO_4$ was toxic to the fungus (292), but others have shown that $(NH_4)_2SO_4$ *per se* is not toxic if the critical acidity is avoided (25). The latter suggest that the toxic factor was the acidity which developed as the ammonium sulphate broke down in the soil.

Root-rots of corn and sugar cane appear to be correlated with high absorption of aluminum (143, 27), and there is evidence that this correlation is dependent upon pH of the soil (209). Aluminum salts were not present in soil solutions where the reaction was higher than pH 5.8, and cases are cited where root-rot was present in soil with pH 4.6 but not when the pH was 6.0. Hoffer has noted the same situation in an Indiana corn field when root-rot was present in soil with pH 5.6 but not with pH 6.2. At the same time McGeorge points out that the relationship of aluminum solubility to root-rot is not the whole answer, since rot is present in many fields which have a pH greater than 5.8 and presumably where aluminum toxicity is not a factor. In this connection it is interesting to recall the case in North Carolina where potash added to soils with pH 3.5 to 5 tended to overcome root-rot, even though the level of aluminum in the soil had not been altered (277). Others have attributed the correction to the fact that potash has the property of greatly decreasing or eliminating the nodal accumulation of iron or aluminum in the plant, thus having the same effect as raising the soil reaction to pH 5.8, at which point aluminum salts become insoluble in soil solution (142, 144). *Pythium* sp.

responsible for root-rot of sugar cane in Louisiana was capable of growing well from pH 5.6 to 9.2, and most of the cane soils were in the neighbourhood of the neutral mark (91). Buchholtz reports that a pH below 6.5 favours root-rot of sugar beets (38), and Zutavern noted heavy damage to sugar beets by *Phoma, etc.*, in sandy clay soils at pH 6.3 to 6.6, while the roots were free from rot in clay sand at pH 7.0 to 7.3. He suggests that control consists in adjusting the soil reaction close to neutrality. In Germany (118) and Belgium (201) also, though black rot is prevalent in acid soils, it is rarely present when soil has a reaction of pH 7 or greater. On the other hand, the heaviest damage from *Phoma* root-rot occurred recently in very alkaline and neutral clay soils (117), whereas the epidemic of 1926 took place under acid soil conditions.

Reinking in New York found pea root-rot destructive in a wide range of soils with reactions ranging from pH 6.25 to 7.48 and in a few soils with a pH of 5.4 and 5.5 (252*a*). Burkholder, on the other hand, has shown that soil reaction has little effect either on the bean plant itself or on its susceptibility to *Fusarium martii* var. *phaseoli.*

Like temperature, the reaction of the soil has a direct effect, especially on the parasites associated with certain root-rots. Moreover, as Doran has shown, the pH of the soil may also directly influence the temperature range at which infection takes place. In addition, soil reaction may play an indirect rôle in its relationship to the accumulation of certain toxic substances that may be absorbed by the plant, thus rendering it more susceptible to attack. Such a correlation has been demonstrated between absorption of aluminum and root-rot of corn and sugar cane.

WATER CONTENT OF SOILS

Water content of the soil is one of the more important factors affecting occurrence and severity of most root-rots. In connection with *Fusarium* rot of pineapple, for instance, one species has been shown capable of invading the tips of roots and killing them when in wet soil, but not when the soil was dry (279). Others report that red stele root-rot of strawberry is more severe in heavy or poorly drained soils, though it may spread from such sections of a field to sections that are lighter or better drained (*e.g.*, 151, 134, 68, 5). In this connection Howells found the disease was evident

first in the lower portions of a field and was commonly associated with a choked drain (151). Hickman writes: "thus, the disease (red stele of strawberries) was worst where soil drainage was impeded. Moreover, as time went on, the symptoms in the diseased plants became more intensified in these poorly drained areas than elsewhere". Excess moisture also favours the black root-rot of strawberry, since it has often been observed to make its first appearance in, and spread from low areas in a plantation. Moreover, strawberries growing at 44°–48° F. in root-rot soil, adjusted to contain 60% of its water-holding capacity, were shown to have clean, healthy root systems (137). However, by gradually increasing both temperature and moisture, the disease became more severe until at 60° F. healthy plants, set in root-rot soil containing 80% of its water-holding capacity, died within a week. At a temperature favourable for the rot, the disease was always more severe in soils containing 80% as compared with 60% of their water-holding capacity. Even at most favourable temperatures for strawberries, plants set in wet soil received a serious set-back.

In connection with root-rot of grapes, Rhoades found *Clitocybe* rot in the low, poorly drained parts of vineyards and orchards where water is liable to stand on the soil, although it may occur in soils underlaid with an impervious sub-soil or hard pan, where natural drainage is poor (253). *Rosellinia* and *Armillaria* rots of the vine produce rapid death of stock in heavy wet soils, while in lighter dry soils the lethal effects may be delayed for several years (181). In Galicia and in all humid and semi-humid regions of Spain *Armillaria mellea* is a serious pathogen of both vine and tree fruits (271).

Pythium aphanidermatum has been found to be severe on watermelons, honeydew melons, quil muskmelons and crookneck squash in rather poorly drained soils, where soil remained very wet for long periods (111), and this same relationship of soil moisture to root-rot is true of peas (67). In 1923 Jones pointed out that "wet soils promoted decay started by parasites (*Fusarium martii* var. *pisi*), though it does not appear to affect in great measure the action of the parasite itself" (162). Again Haenseler found that though root-rot of peas caused by *Rhizoctonia solani* was present in soils having from 5% to 80% of their water-holding capacity, the least injury was produced at 40% (119). There is also evidence that *Aphanomyces* root-rot of peas develops most aggressively in low,

poorly drained soils and in heavier soils which are high in water-holding capacity (331), as well as in soil which is naturally retentive of water or in which water is held by reason of impervious layers (161). Moreover, in heavier soils the parasite may persist for at least six years after it has become abundant, while in light soils its period of survival may be shorter. In a survey of root-rot of peas in 1924 we read that "in approximately one half of the fields inspected the disease due to *Aphanomyces euteiches* was found in more moderate quantity, frequently being present in severe form only in situations unduly wet as a result of inadequate drainage or proximity to water courses" (74). More recently *Aphanomyces* root-rot of peas was revealed as being favoured by high soil moisture, since no rot occurred in naturally infected soil when the moisture was maintained at 45% of its water-holding capacity, while at 75%, 72% of the plants became infected (287).

Low soil productivity and soils either too dry or too wet seem to favour late root-rot of sugar beets with which *Phoma betae* and *Fusarium* spp. are associated (288). In this connection *Phoma* rot was benefited by drought "which especially during June appears to create a dangerous period in the life of the beet, since an early drought reduces the vitality of the beets so much that they fail to recover and later succumb to late blight and root rot" (256). Le Clerg reports that *Rhizoctonia* root-rot of sugar beet is favoured by low soil moisture (190), and Young, using soil temperature tanks, found the lowest incidence of black root and the best beets developed at 54° and 61° F. in the slightly dry and slightly wet soils (342). Others noted that drainage was beneficial in the reduction of sugar beet damping-off or black root (*Pythium* spp., *Rhizoctonia* spp. and *Aphanomyces* spp.) and that good results were obtained by growing the plants on ridges with furrows on both sides (57).

Root-rot of sugar cane, too, is favoured by poor drainage conditions (77), and in Cuba such predisposing factors as lack of drainage, lack of moisture, deficient cultivation and deficient fertility are all associated with the general complex (84). A high water table combined with fine texture of soil and low winter and spring temperatures are probably the chief conditioning factors of severe outbreaks on present commercial varieties of sugar cane in Louisiana (247). Flor also points out that root-rot of sugar cane caused

by *Pythium* sp. is more severe in soils at 50% or more of their water-holding capacity (91), and it has been favoured by abnormally high early winter temperature followed by alternate wet and dry periods (245). Ciferri, in a publication on mycorrhiza in relation to root-rot of sugar cane, points out that any factor which hinders rapid formation of new roots, favours an outbreak of rot, and he mentions in this connection excessive moisture, severe drought and other factors.

Excessive moisture, high temperature and poor drainage have been found to favour root-rot of peppers caused by *Phytophthora capsici* (311). *Phytophthora* root-rot of sweet clover was most abundant in low, wet portions of fields (163), and low, poorly drained areas favoured root-rot of cauliflower caused by *P. megasperma* (308). Petri notes that excessive soil moisture should be avoided by drainage in combating *Phytophthora* root-rot of citrus (236).

The violet root-rot of tea, due to *Sphaerostilbe repens* B. & Br., is stated to be associated with water-logged and acid soils (318), while the same fungus causes a red rot of limes in St. Lucia only in poorly drained orchards (332). In the Sudan a root-rot or wilt caused by a fungus complex was associated with years of high rainfall and soils of alkaline content (203), and elsewhere a root-rot of chestnut and beech was associated with impeded drainage in the sub-soil (65).

It thus becomes clear that root-rots in general are aggravated by excess soil moisture, though it should be realized that factors other than lack of aeration are connected therewith, since toxins, including hydrogen sulphide, soluble aluminum, iron and manganese compounds and organic substances, may occur in poorly aerated soils. Experimental evidence indicates that aeration of the soil produces no obvious difference in the amount of root-rotting, thus suggesting the presence of some factor or factors in addition to excess water. Others have shown that salicylic aldehyde predisposed sugar cane roots to infection by *Pythium arrhenomanes,* with reduction in weight from two to seven times as great as that caused by the fungus alone (248).

In the above résumé of the literature dealing with the correlation of soil moisture to root-rots, it is apparent that practically all rots are favoured by excess soil moisture. This is readily understood

when it is recalled that most soil fungi are favoured by abundant soil moisture, whereas the roots of plants are adversely affected by the same condition, since roots require good aeration to function normally. Hence excess water renders the host more susceptible and favours the growth of the soil flora in general. Moreover, in water-logged or poorly drained soils toxins accumulate which apparently increase the susceptibility of the host and encourage root-rot attack.

CONTROL

Root-rots, largely because of the complex nature of their environment, are most difficult to control, except in those few cases where resistant varieties are available. Still much can be done to lessen the losses caused by these diseases. The most general means of control consists of planting healthy stock, supplemented by crop rotation, certain cultural practices, fertilization and cover crops. Where the rots are seed-borne, such as those of peas and beets caused by *Ascochyta* and *Phoma,* respectively, seed disinfection is of value. In addition, there are many miscellaneous measures of value in connection with certain specific rots which will be mentioned.

Varietal resistance. Obviously the ideal means of controlling root-rots is by use of resistant varieties, but, though some progress has been made along this line, especially in connection with brown root-rot and black root-rot of tobacco, there are as yet few rots where this means of control is available, due to the lack of suitable resistant varieties. Peglion in Italy in 1897 was the first to appreciate the possibility of controlling black root-rot by means of resistant varieties. Since then, breeding and selecting for resistance has been under way, especially in Italy, the United States and Canada. In 1916 James Johnson studied resistance to black root-rot in white burley and cigar-leaf tobaccos and found that Little Dutch and Connecticut Broadleaf were most resistant. In 1930 he published on the genetics involved in resistance to the disease. In the United States to-day breeding and selection for resistance to root-rot is being carried out, especially in Wisconsin, Kentucky, Virginia, Connecticut, Maryland, Tennessee and North Carolina. In Canada, it centers mainly in Ontario at Ottawa and Harrow. Some of the resistant varieties listed in the United States are Havana 142, Round Tip, Maryland Standup Resistant, Johnson resistant White

Burley, Kentucky No. 5, Kentucky 16, Standup Burley Mammoth, Yellow Special and Special 400. These varieties or strains are being used in connection with present breeding programmes (98). In Canada the list of varieties in order of degree of resistance to black-root is (21) : Gold Dollar 82C, Yellow Mammoth, Duquesne, Bonanza, White Stem Orinoco and White Mammoth of the flue-cured varieties, and Harrow Velvet (developed at Harrow Station), Kentucky No. 16, Halley's Special, Type No. 5, Gay's Yellow, Kelley and Judy's Pride of the burley type of tobacco. Of the cigar binder types, Resistant Havana, Havana 211, Havana 236, Connecticut Broadleaf (William), Comstock Spanish Pomeroy and Connecticut Havana No. 38, and of the pipe varieties, Grand Rouge, Belge, Rose Canelle, Parfum d'Italie, Obourg de Vincent, Petite Havana and Canelle, are listed. In connection with brown root-rot, the burley varieties Kelley and Judy's Pride are more resistant than Harrow Velvet, Halley's Special, Kentucky White Burley, Gay's Yellow, *etc.*, while of the flue-cured varieties White Mammoth, Bonanza, White Stem Orinoco and Duquesne appear to be more resistant than Yellow Mammoth, White Stem Willowleaf, Adcock, Jamaica Wrapper, *etc.* (175).

In this connection it is interesting to note that certain varieties resistant to black root-rot may be particularly susceptible to brown root-rot, and *vice versa.* For example, the Harrow Velvet variety, outstandingly resistant to black root-rot, appears to be one of the most susceptible varieties to brown root-rot. Valleau in 1925 was possibly the first to present evidence to the effect that a strain of tobacco resistant to black rot might be susceptible to the brown (320).

Recently Reid, reporting on the general research carried out since 1929 by the Department of Agriculture for Scotland on the red stele or red core root-rot of strawberries, states that five seedling varieties (Auchincruive 1, 2, 4, 5 and 6) have shown striking resistance to this rot in England, Illinois and Maryland. The American variety Aberdeen is also resistant in Scotland and America. In breeding for resistance to this disease in America, many promising seedlings were obtained and four hybrids selected, all crosses between Aberdeen and Fairfax, that are immune and commercially promising (153). Other hybrids of interest in this connection were a cross between a Scottish selection BK–46 and Fair-

fax; Aberdeen x Mastodon selection; Aberdeen x Blakemore selection and Aberdeen x Dorsett.

In research over a period of years at St. Catharines, Ont., it was demonstrated that the native wild variety *Fragaria virginiana* was much more resistant to black root-rot of strawberry than were the commonly grown horticultural varieties. Of these, the Premier variety appears the most susceptible, while Blakemore shows slight resistance (137).

Increased resistance to root-rot of sweet clover by means of selection has been reported (163), and in recent other studies relating to varietal resistance of alfalfa and sweet clover to root- and crown-rots, *Medicago falcata* showed the highest resistance to *Cylindrocarpon Ehreubergi* Wr. and *Sclerotinia sativa* Drayton & Groves, while sweet clover varieties belonging to *M. officinalis* showed more resistance than those of *M. alba* to *S. sativa* (60). A strain of Alpha sweet clover, developed at Saskatoon, was quite resistant to *Phytophthora cactorum.*

Considerable work has been done in connection with breeding and selection for disease-resistant sugar cane, and the following commercial varieties have been cited as being resistant to root-rot: C. O. 290, C. P. 807, C. P. 28/11 and C. P. 29/116 (247).

J. L. Weimer found hairy, smooth, light-seeded Hungarian vetches and *Vicia hybrida* to show considerable resistance to root-rot (*Aphanomyces, Pythium, Rhizoctonia, Fusarium* spp., *etc.*), whereas woolly pod, Monantha and common vetches (*V. sativa*) were quite susceptible. He reports that no variety of pea is resistant, a fact which has been confirmed by many others. On the other hand, there are many varieties of peas which show resistance to wilt caused by *Fusarium orthoceras* var. *pisi.* In this connection 12 varieties are listed as being resistant under Wisconsin conditions (331).

It is interesting to note that though some 1700 species of plants are susceptible to the cotton root-rot fungus, monocotyledonous plants, *e.g.,* corn, onions, cannas and certain grasses, are highly resistant or immune. This resistance is explained as being due to the presence in such plants of an ether-soluble toxin or toxins, possibly organic acids or esters (82). In this connection it has been demonstrated that resistance of some species is associated with the presence in those plants of certain alkaloids (113, 115), and that

phenolic acid and related compounds are toxic to *Phymatotrichum omnivorum* (114). Certain plants, especially in Ranunculaceae, Berberidaceae, Fumariaceae, Leguminosae and Lolanaceae, have shown a correlation between the presence of alkaloids in them and their resistance rating to *P. omnivorum* (112). Though no variety of cotton has proved to be consistently resistant to root-rot, several legumes, such as sesbania and guar and some varieties of cowpeas, appear to be highly resistant.

Though some have found no evidence of resistance in *Malus* spp. to *Xylaria mali* (93), another investigator noted that suppressed or weakened trees were more susceptible to attack by this fungus (33). Barss reports French pear root stocks (*Pyrus communis*) and the northern California black walnut stocks to be highly resistant to *Armillaria mellea,* while the common English walnut is very susceptible. Kesseler says that Wild Brazil, Pernambuco, Congo and Ruby pineapple varieties show resistance to pineapple root-rot (*Nematosporangium* (*Pythium*) *rhizophthoron*), while the Cayenne variety is susceptible. In three hybrid varieties, the parents of which were also tested, he found that susceptibility was intermediate between that of the parent forms.

Crop rotation. As Garrett (104) states, "crop rotation is one of the oldest methods of controlling soil-borne diseases and is dependent upon specialization of parasitism in the pathogenic organisms. Its value becomes restricted with increase in host range of the parasite, so that the control of such a fungus as *P. omnivorum* with a known host range of 1700 species by crop rotation severely curtails the range of possible crops which can be safely grown". It is obvious also that a much longer period of rotation will be required when the organism to be controlled produces thick resting spores or sclerotia, than when such forms are not involved. Indeed, large numbers of viable sclerotia of *P. omnivorum* have been found in soil after 12 years of continuous cropping with non-susceptible cereals, and after the same period of clean fallow (262).

Moreover, certain fungi associated with root-rots are capable of existing as saprophytes on organic matter in the soil, thus necessitating a much longer period of rotation, if not actually eliminating this method, in some cases at least, as a satisfactory measure of practical control. In this connection, *Fusarium culmorum* (W. G. Sm.) Sacc., a well known parasite of cereals and other crops, was

the dominant fungus associated with early decomposition of buried wheat straw, thus indicating that it has a saprophytic as well as a parasitic stage and hence is not apt to respond readily to crop rotation (266). It is sometimes impossible to grow flax susceptible to wilt (*Fusarium lini* Bolley) more than once in 10–12 years (13), and survival periods of 11 and 14 years have been found for *Fusarium conglutinans* Wollenw., the cabbage yellows organism (215, 166). In the tropics, species of *Rosellinia* are capable not only of growing as saprophytes through dead leaves and other decaying vegetable matter in or on the surface of the soil, especially in shady or damp situations, but of parasitizing tea and other plantation crops with which they come in contact in the course of their growth through the surface litter (94, 318). *Pythium arrhenomanes,* too, remains active in the soil at least four years and has not been controlled by ordinary two to three-year rotations or fallow (80). Notwithstanding the above and other adverse factors, crop rotation has proven itself an essential practice in the control of root-rots. For instance, *Pythium* rot of sugar cane is generally of little importance throughout the sirup-producing sections of Alabama, Florida, Georgia and Mississippi, apparently because of the long rotation (3 to 5 years) of crops (non-susceptible) commonly followed, and in southern Louisiana the common practice of a one-year rotation of sugar cane with a legume is not long enough to prevent root-rots being of major importance (247). *Aphanomyces* root-rot of peas can be prevented and controlled most effectively by crop rotation. The length of rotation varies, however, with local conditions. For instance, on certain irrigated soils with low moisture-holding capacity, root-rot is lacking or has not become destructive even after peas have been grown nearly every year for ten years. On the other hand, the disease has become destructive on similar soils when they were sub-irrigated. Moreover, on some soils in humid territory the third successive crop of peas is often badly damaged by this rot, and a comparatively long rotation appears to be necessary to prevent it from accumulating in the soil. In this connection it is to be noted that a six year rotation has been insufficient for soils that were heavily infected (164).

Leach reports that a two to four-year rotation of sugar beets with cereals, or winter crops of peas, spinach or lettuce reduced

Sclerotium rolfsii to safe levels, but this was not the case when sugar beets were rotated with summer crops of beans, on account of both susceptibility to pathogens and their cultivation during the summer when higher temperature favoured the fungus concerned (183). Similarly, flax following sugar beets was subject to attack by *Pythium* spp., since both crops are susceptible to these fungi (273). In connection with the *Phoma* root-rot of sugar beets, the disease was most prevalent where crop rotation was neglected, and the best crop preceding sugar beets was peas (117). Campbell states that black root of sugar beets (*Rhizoctonia* sp., *Pythium* sp. and *Aphanomyces* sp.) can be controlled by proper rotation. He recommends that a cultivated crop such as beans, corn or potatoes intervene between a sod and a beet crop. Root-rot of sugar beets caused by *R. solani* was not present in beet fields preceded by four years of grain (207), while sugar beets following potatoes developed less rot than when sugar beets followed sugar beets (192).

It is well recognized that black root-rot of strawberry is more severe when strawberries follow strawberries (137); hence the recommendation to rotate strawberries with some other crop. It is further recommended that when practical, strawberries be planted on land that has never grown them, since it has been the experience of all investigators that root-rot is rarely present the first or second year on such soil.

In Java, it is recommended, at least three years should elapse between crops of sugar cane on the same soil (179). Investigations on root-rot of flax caused by *Thielaviopsis basicola* recommend two successive root crops previous to the flax (234). Corn in Missouri should not be grown more than two years in five on the same soil (30), and infection by *Pythium* root-rot appears reduced when soya beans precede corn in the rotation, but increased when the corn is preceded by timothy (258).

In connection with *Fusarium* root-rot of clover, Young suggests temporary substitution of a non-susceptible leguminous crop such as soya beans. Others recommend rotation and drainage of soil as essential in preventing root-rot of peas caused by *Aphanomyces euteiches, Pythium* spp., *Fusarium* spp., and *Rhizoctonia* spp. (74, 290, 196, 164). However, a three-, four- or five-year rotation did not entirely eliminate pea root-rot, though the population

of the pathogens in the soils was reduced (252*a*). Pugsley, in advising on prevention of root-rot of onions caused by *Fusarium* spp., also recommends crop rotation and sanitation.

In connection with root-rot of cotton, a two-year fallow with a rotation of non-susceptible crops (212) or tillage operations that will reach the sclerotia as a supplement to fallow and rotation (213), is advised. A two- or three-year rotation with grains combined with deep tillage may also be effective (171), and the general principle of fallow and crop rotation is advocated by numerous other investigators (260, 292, 250, 298, 167, 62).

In a testing of the influence of the cropping system on tobacco, brown root-rot was prevalent following timothy, clover, corn and hay and only slightly less following potatoes (165, 159). In Ontario, when timothy, corn or soya beans preceded tobacco, brown root-rot was more prevalent and severe (175). In the end decomposition of corn and timothy infusions some toxic agency or agencies appear to be liberated which tend to induce brown root-rot, and other crops which do not induce the rot under field conditions likewise do not do so during the various stages of decomposition under laboratory conditions (71, 78, 79). Also, brown root-rot appears to be less severe in tobacco after a crop of lucerne or alsike clover than after timothy (71).

Biological control. The present status of toxins in relation to root-rots has recently been reviewed (107), and the same subject discussed in connection with the general aspect of biological control (104). The principle of biological control is based on the fact that the soil population is in a dynamic biological equilibrium. Therefore, factors which favour the build-up of saprophytic organisms are likely to upset the balance to the disadvantage of the parasitic forms and to result in a reduction of disease. This end may be accomplished in various ways, as by green manuring, manuring, changing pH, clean fallow and use of chemicals. Green manuring or addition of sufficient organic matter to the soil has been demonstrated by many investigators to have a beneficial effect on certain crops affected by *Actinomyces scabies* (Thaxt.) Güss. (218, 219), *Ophiobolus graminis* Sacc. (90, 100–102), *Phymatotrichum omnivorum* (172) and black root-rot of strawberries in which several organisms are associated (139).

Canadian workers (especially 270, 33, 34, 132) and others (305, 75, 76, 173, 335, 336) have presented evidence that certain organ-

isms are antagonistic to specific parasites and capable, under suitable conditions, of effecting reduction of disease. Clean fallow was beneficial in connection with cotton root-rot (211) and with *Helminthosporium sativum* and *Ophiobolus graminis* (269), and, though the method whereby this reduction was effected is not clearly understood, it would appear likely (107) that certain antagonistic effects—conditions unfavourable for the parasite or lack of food for the parasite under summer fallow conditions—may be factors of importance.

The effectiveness of organic manure in checking root-rots is generally explained by the hypothesis that addition of large quantities of green plant material increases the numbers and activity of saprophytic forms at the expense of parasitic forms which supply, in part, the nitrogen required for the decomposition process. In addition, a qualitative as well as quantitative effect on the soil microflora may be involved when green manures are turned under as shown by a preponderance of fungi in the roots of tomato, soya beans and corn. The predominating fungi were *R. solani, Thielaviopsis basicola* and *Pythium* spp., respectively (139). If the biology of the soil is in a dynamic equilibrium, then the buildup of specific fungi must effect the balance of other groups. That it is possible to affect the soil flora in this way is indicated by the fact that turning under soya beans reduced the incidence of root-rot of strawberries (139). However, the principles underlying this beneficial result have yet to be investigated.

Several investigators have presented evidence to the effect that ammoniacal nitrogen may be toxic to certain fungi, thus suggesting the possibility of using ammonia-yielding compounds for control of cotton root-rot (226, 227). Streets recommends ammonium sulphate (292), and increases of five to nine tons of sugar beets per acre by application of it have been secured (185). It was not determined, however, whether the beneficial results were due to toxicity of the ammonia or to the influence of the nitrogenous fertilizer upon the host. More recently, from 1934 to 1937 nitrogenous fertilizers gave a consistent reduction in rot of sugar beets caused by *Sclerotium rolfsii* (186). In explanation thereof it was suggested that either nitrogenous fertilizers may effect changes not only in the metabolism of the fungus, reducing its growth or pathogenicity, but also in the host itself, possibly increasing its resistance,

or the fungus may be depressed as a result of a change in the balance of the soil flora. In this connection there was experimental evidence to the effect that low concentrations of ammonia are toxic to the mycelium and sclerotia of *S. rolfsii.* However, since ammonium sulphate in alkaline solution and calcium nitrate in solutions of similar concentrations were only mildly toxic and harmless, and since all three materials gave equally good results in field trials, the authors suggest that the control obtained in the field may have been due to factors other than ammonia toxicity. Likewise, Blank and Talley question that ammoniacal compounds *per se* are toxic, since they found that ammonia nitrogen is a good source of nitrogen for *P. omnivorum.* They suggest that the beneficial results from ammonia compounds may be due to a growth response to the additional nitrogen and/or the acid condition which results from application of such compounds (*cf.* section on Reaction of Soil, above).

More recently (1941) Henderson, in studying the value of certain nitrogenous compounds as disinfectants for tobacco seedbeds, found that *Thielaviopsis* root-rot of tobacco could be controlled effectively by application of urea to the soil at the rate of ½ lb. per square yard. However, when ¼ lb. urea was used the rot was severe, though at the end of the experiment the soil showed a reaction of pH 8.00 in comparison with pH 8.65 in the soil treated with ½ lb. of urea. This would suggest that the greater accumulation of ammonia in the soil where ½ lb. was applied, was responsible for the sterilizing effect, and not the slight difference in pH reaction. Additional evidence that this was the case was obtained with studies in the laboratory which showed that a concentration of ammonia as high as 93 mgms. ammonia-nitrogen per 100 grams of dry soil at a pH of 8.1 was sufficient to prevent growth of *T. basicola.* The above concentration of ammonia was found by analysis of seedbed soil to be present in the urea (½ lb.) treated soil. Thus Henderson's results in the soil treated with ½ lb. of urea support the contention that certain ammonia compounds may be toxic to certain fungi. Others suggest that the beneficial results of ammonia compounds may be explained on the basis that root diseases are toxin-induced and that the basic nitrogen in ammonia antidotes the toxin (149).

Fertilization. Sardina and Landaluce claim that *Armillaria* root-rot of the vine can be controlled only by preventive measures

which, in addition to extirpation, deep cultivation and drainage of the holes, should include replacing of stable manure with well-balanced mineral fertilizers (271). In Louisiana nitrogenous fertilizers increased *Pythium* root-rot of sugar cane, while high phosphate treatment reduced it, and neither nitrate nor phosphate had any marked effect on the antibiotic action of *Trichoderma* spp. against *Pythium* (189). This same relationship of nitrate to *Pythium* root-rot was also reported from Coimbatore (243) and the United States (247).

On the other hand, marked control of *Aphanomyces* root-rot of peas was obtained under greenhouse conditions with one application of 4–16–4 fertilizer at the rate of 500 lbs. per acre (330). In field plots, where the fertilizer was applied with the seed, increases in yield from 46% to 248% were obtained over control plots. It appeared that quickly available nutrients in amounts of 200 to 300 lbs. per acre in the furrow with the seed made it possible for the plants to develop greater resistance. Much greater reduction of rot and increases in yield were secured when 2% of readily available nitrogen was included in the fertilizer than when it was omitted. More recently there is evidence that the nitrogen fraction is more active in reduction of pea root-rot than either the phosphorus or potash content when 2–12–6 fertilizer is used (287). In New Jersey root-rot of peas was reduced by heavy applications of hydrated lime (4000 lbs. per acre), but lesser amounts had no inhibitory effect (120), and elsewhere incidence of the rot was delayed and injurious effects on the host greatly reduced by use of 1000–2000 lbs. of complete fertilizer per acre (121). Greenhouse tests indicated that nitrate of soda, sulphate of ammonia and muriate of potash were more effective than was superphosphate. Reinking in New York states that in favourable growing seasons, profitable yields of peas were obtained where soils were sufficiently fertilized (600 lbs. per acre of a 5–20–5 or 10–20–10 fertilizer) in spite of the presence of pathogens in the soil (252*a*).

Reduction in root-rot of sugar beets has been reported with application of commercial fertilizer containing 100 lbs. nitrogen per acre (183), and promising results in control of black-root of sugar beet were secured by incorporation with the seed of liberal amounts of phosphate fertilizer—three to four times the customary dose of 100 or 150 lbs. per acre (57). More recently, experiments from

1934 to 1937 in the Sacramento Valley, California, showed that application of nitrogenous fertilizers gave a consistent reduction in *Sclerotium* root-rot of sugar beets (186).

It is considered that root-rot of Coco-yams may be due to lack of potash. Therefore, presumably, addition of potash would be of value as a corrective (341). Soil deficiencies, especially of potash, and accumulation of aluminum and iron compounds in corn appear to render the corn plants more susceptible to root-rot (143, 199).

In France an investigation of the composition of soils in which fruit trees and vines suffered from attacks of *Armillaria mellea* indicated that such soils were poor in carbonate of lime (97). Previously Gard (96) had expressed the opinion that a deficiency of carbonate of lime was the chief factor pre-disposing walnuts to attacks by *A. mellea.*

Use of commercial fertilizers in controlling root-rot of cotton has been studied by many investigators. Though there is evidence in some sections of response from using nitrogen and phosphoric acid in combination, the results in general have been inconsistent and not convincing. Incidence of the rot on light, sandy loam was reduced by nitrogenous fertilizers and increased by those containing phosphorus, while on heavier soils the effect was less pronounced (168). Ammonia salts, *e.g.,* sulphate and phosphate, were toxic to *Phymatotrichum omnivorum,* and the sulphate was definitely beneficial to certain infected trees and could be applied with success to small areas of infection in cotton and alfalfa fields (227, 292).

Disinfection of soil. Disinfection or sterilization of soil is a most satisfactory method of overcoming root-rots, but not practical except for small plots or seed and plant beds. Sterilization of seedbed soil by means of steam or chemicals, especially formalin and chloropicrin (50, 52, 109, 194, 210, 343), is common practice in many districts, particularly for black root-rot of tobacco and root-rot of sugar beets. In addition to use for disinfection of seedbeds, various chemicals have been recommended as auxiliaries. For instance, there is the removal of vines infected with *Rosellinia necatrix* or *Armillaria mellea* and disinfecting the soil under such vines with carbon disulphide or formalin (181). Thomas and Lawyer have also recommended carbon disulphide in connection with *A. mellea* (302). They report a kill of the fungus to a depth of 60″ under a wide range of conditions when 45 cc. of carbon disulphide is ap-

plied 8″–9″ deep at 18″ staggered intervals. They say that eradication of the fungus from orchard soils seems possible if applications are made under ideal conditions, that is, low soil moisture and a surface blanket of moistened soil. In connection with a root-rot of forced tulips, treatment of the soil previous to planting with steam or formalin yielded 99.5 and 97%, respectively, of marketable bloom, while Cheshunt compound gave unsatisfactory results (39). Howells (150), reporting on a *Phytophthora* root-rot of glasshouse tomatoes, recommends cutting away affected roots while plants are in pots, to about ½″ above the level of decay, repotting and watering with mercuric chloride solution (1 oz. per 20 gal.), nitrate of soda being applied two days later. Esmarch recommends for small areas removal and burning of affected plants, combined with soil disinfections by means of a 1% solution of formalin or Uspulum to control violet root-rot (*Rhizoctonia violacea* Auct. Amer.) of clover, lucerne, turnip and asparagus.

In black-rot of sugar beets satisfactory control of late pre-emergence and post-emergence rot was obtained by using cyanamide, 135 lbs. per acre, a week before planting (42). In addition, Campbell and many other investigators have demonstrated the value of seed treatment in connection with this disease. In so far as seed treatment for control of black-rot (blackleg) of sugar beets is concerned, there is conflicting evidence, though the bulk of evidence favours it. Many have reported on the value of seed treatment (241, 263, 42, 106, 232, 178, 289, 201, 340), though Campbell found no evidence of protection after the plants had emerged, and there is a report of beneficial results on the lighter type of soil with none accruing on certain heavier types (58). In this connection Stirrup has shown that when seedlings are growing under adverse conditions, seed treatment exercises a certain amount of control, but when conditions are favourable for growth, little or no benefit accrues from such treatment. Appel in 1929 also reported on unsatisfactory results from chemical treatment, but beet plots in California on which ammonium sulphate or ammonia were added to the irrigation water showed less than 1/3 of the *Sclerotium* (*rolfsii*) root-rot found in the controls, and cyanamide worked into the soil three weeks before planting, reduced the incidence of infection by some 50% (182). In Italy Petri recommends drainage and manurial dressings, counterbalanced by application of phosphate, for

prevention of *Phytophthora* root-rot of citrus (236). He states a cure may be effected by laying bare affected roots, pruning, removing all dead and diseased roots, cutting away the necrosed parts of the collar and disinfecting the surface with a 25% to 30% solution of ferrous sulphate or a 2% to 4% solution of copper sulphate and lime. After drying, the wounds should be painted with pitch or carbolineum. In replacing a diseased tree he recommends removal of the old roots, the cavity to be left open for a year, and application of 2% Bordeaux mixture, 5% solution of formalin or quicklime.

Organic manures. In Arizona King (171, 172) recommended burying, during the winter, large quantities of organic matter in deep furrows in the affected areas. The ground is irrigated to encourage rotting, and cotton is planted in the spring over the decayed organic matter. Control increases with successive treatments, since this practice builds up an abundance of active saprophytic organisms, a condition which is not favourable to *Phymatotrichum omnivorum.*

Incidence of strawberry root-rot appears closely correlated with soil treatment, for plants grown in sterilized soil and soil in which soya beans had been incorporated, remained free from disease until the third season, while those in soil following manure, corn, red clover and timothy all became diseased, the severity of attack increasing in the respective series in the order named (139). In small outdoor plots at St. Catharines over a two-year period yield increases of 525 and 825 quarts per acre have been obtained when strawberries were grown in plots in which one or two cover crops of soya beans were turned under, respectively, in comparison with similar plots in which strawberries were ploughed under.

In explanation of this beneficial action, decomposing soya beans may undergo a carbohydrate breakdown which favours accumulation of innocuous fungi at the expense of pathogenic forms (337). This same beneficial effect was produced in root-rot soil by substitution of glucose for soya beans. When red clover was incorporated with the soil, a putrefactive decomposition took place with no beneficial shift from a root-rot standpoint in the biology of the soil.

Ringing, felling and barriers. In connection with control of *Armillaria* and *Rosellinia,* use of trenches has been recommended to delimit affected trees or areas (14). Open trenches have been used also for checking the spread of *Phymatotrichum* root-rot of

cotton. In addition, artificial barriers, such as galvanized iron, or chemical barriers, such as crude oil, sulphur, sulphuric acid and copper sulphate, have given satisfactory results in checking this same disease. It is stated that the chemically treated soil barriers are successful and practical. The soil is removed to a depth of 30 inches and a width of 6 inches, mixed with the chemical and replaced. Barriers 4 to 6 inches wide, in which 2 to 4% of sulphur had been incorporated with the soil, prohibited the fungus from crossing the barrier. The treated soil constituting the barriers became as acid as pH 2.2, while outside the barrier it remained around pH 7.5–8. Four or more rows of sorghum acted as effective barriers (296).

Ring-barking affected trees as a measure of controlling root-rot has been recommended for *Armillaria* and kindred types. Leach, studying *Armillaria* root-rot of tea in Nyasaland, observed that the hyphae developed freely in the xylem and pith and not at all in the cortex of seedlings, suggesting that the fungus requires abundant supplies of carbohydrates (187). It was also found that the roots of normally felled trees were high in carbohydrate content, and it seemed feasible, therefore, that if trees were bark-ringed before felling, to prevent passage of carbohydrates to the root from the leaves, such roots would be less susceptible. An experimental test supported this hypothesis. Examination of 240 felled trees (unringed) showed that 54 were affected by a dry rot and 186 showed *Armillaria* rot. Of 18 trees ringed before felling there was only one doubtful case of *Armillaria* rot. More recently Leach expressed the opinion that the rate at which roots die after a tree is felled is the factor controlling distribution of *A. mellea* in cleared forests, and accordingly ring-barking of deciduous trees should be effected just after breaking into leaf (188). He recommends that trees which die slowly after ring-barking should be felled one year after ringing. Forbes, also working in Nyasaland, recommends that trees and shrubs on all land to be cleared for planting to tung trees, be ring-barked at least 18 months before planting operations, as a preventive against collar crack (*A. mellea*). Gadd in Ceylon also found the practice of ring-barking felled trees promising as a means of protecting the tea crop from infection of *Poria hypolateritia* in jungle clearings (95). Napper has found that stump injection with sodium arsenite is advantageous in control of *Fomes* root-rot

of *Hevea* rubber, since it hastens decay and invasion by saprophytic fungi, thus reducing chances of infection by and spread of *Fomes lignosus* Klotzsch. in the replanted stand (223, 225). This is, in fact, the basis for girdling or felling as practised in connection with root-rots where inoculation comes from root infection in indigenous forests or plantings to be replanted. All these measures aid in rapid decomposition of roots and stumps, thus favouring decay organisms at the expense of parasitic fungi.

Miscellaneous measures. Another rather unusual means of controlling root-rots involved planting a mixture of three different indicator plants in areas to be replanted to *Hevea* rubber in Ceylon (23). The value of this method lies in the prompt spotting of indicator plants affected with rot and the removal and burning of all infected material.

In California infection by *Sclerotium rolfsii* was 2.4 to 4.2 times as great in unthinned sugar beet plots as in plots thinned to produce a uniform stand of single plants (184).

Certain tropical species of *Rosellinia* are capable of spreading through leaf mold (94) on the surface of the ground, and Gadd recommends in a wet season the removal of such litter, especially from around the main stems of tea bushes. He points out that in dry seasons there is little chance for the fungus to spread as noted above. Tunstall states that liming the soil and exposing the collars of tea bushes often checks the spread of *Rosellinia.*

Though rogueing is not practised generally in connection with root-rot control, it has given some success in relation to certain tropical root diseases of plantation crops in Malaya. Thus Napper has found rogueing of value in connection with control of root disease on rubber caused by *Fomes lignosus* and *F. noxius.* He also reports that tree to tree collar inspection of rubber trees, accompanied by digging around infected trees to expose and remove diseased roots, has resulted in low incidence of infection at a very low cost (224).

TYPES OF ROOT-ROTS

In the foregoing résumé it is clearly indicated that several different fungi may be involved in the production of root-rot on certain hosts. The question naturally arises as to whether it would be preferable to look upon such a rot as a single disease, though several fungi may be involved, or to take the view that each fungus of the

group associated with the rotting should be considered as the cause of a distinct root-rot, even though there may be no macroscopic means of distinguishing between them. Both views are at present recorded in the literature. If the former be accepted—the weight of evidence is in its favour—then root-rots may be classified into three general groups: Type 1. Simple root-rot. This is the type where a specific organism is responsible for a rot, such as the *Xylaria, Armillaria* or *Clitocybe* rots of apple, and *Phymatotrichum* rot of cotton and other plants. Type 2. Compound root-rot. In this type, though there is a specific organism of prime importance, other fungi are commonly associated with it and aid in producing the rot as it occurs in nature. Examples of this type are the *Pythium* root-rots of sugar cane and corn, *Aphanomyces* rot of peas, and possibly *Thielaviopsis* rot of tobacco. Type 3. Complex root-rot. In this type no specific fungus is alone constantly associated with the diseased condition, but a complex of fungi and other organisms is involved, no one of which appears to stand out as being primarily important. In this category would be placed the black lesion type of root-rot of strawberry in England (20) and Ontario (135, 313) and raspberry root-rot in Ontario and British Columbia (18).

At this point it might be well to consider the time factor or sequence in which fungi become involved in certain complex root-rots. There is evidence to the effect that *Pythium deBaryanum* is the primary parasite involved in root-rot of corn, followed by *Pythium graminicola, Gibberella saubinettii, Rhizoctonia solani, Helminthosporium sativum, etc.* (140); hence this rot is reported as the *Pythium* root-rot of corn. Respecting root-rots of strawberry and tobacco seedlings, the sequence of fungi involved varied with the soil (138). For instance, in muck soil strawberry roots became infected with *Thielaviopsis basicola* in 18 to 24 hours, whereas tobacco roots did not show the fungus until the fourth day following germination of the seed. In strawberry, however, no necrosis took place, nor did infection spread beyond the incipient stage. Following this incipient infection in muck soil, *Pythium* sp., *R. solani,* the Phycomycetous mycorrhizal fungus, orchid rhizoctonia, nematodes and *Asterocystis* were observed in tobacco roots, while *R. solani,* Phycomycetous mycorrhizal fungus, orchid rhizoctonia and *Pythium* species were in strawberry roots in the order

given. In a strawberry root-rot soil, however, the sequence was as follows: in tobacco roots—orchid rhizoctonia, nematodes, *R. solani, Pythium* spp., phycomycetous mycorrhizal fungi, *Asterocystis;* in strawberry roots—*R. solani,* nematodes, orchid rhizoctonia, *Pythium,* phycomycetous mycorrhizal fungus, *Asterocystis.* In this connection it is most interesting to note that of the many genera and species of fungi present in a soil, only a comparatively few are commonly associated with root-rots of different host plants. As is to be expected in a complex root-rot of this type, in which the fungi concerned are facultative parasites, the sequence of fungi is not necessarily always the same, since the sequence is affected by variations in soil type, soil flora, temperature, moisture, pH reaction, *etc.* For instance, microscopic examination of the roots of chrysanthemums, roses, gladioli and tulips affected with a root-rot complex indicated a changing fungous flora in the roots throughout the season (19).

TRENDS IN RESEARCH

Obviously the earlier researches on root-rots of crop plants were concerned for the most part directly with host parasite relations and control. With the availability of the Cholodny method and the lacto-phenol and similar techniques for direct microscopic examination of roots, considerable research, especially by Canadian workers (18, 138, 174), has been directed to the general flora as found in affected roots. This aspect has greatly increased our knowledge of the natural root flora and has enlarged our concept of "complex root-rots", that is, complex in the sense that several organisms may be associated with certain rots. For instance, even in the case of *Thielaviopsis basicola,* recognized as the causal agent of black-rot of tobacco, other fungi, especially the so-called phycomycetous mycorrhizal fungus, *Rhizoctonia* spp., including *R. solani, Pythium* spp., and nematodes may be associated in the roots with the primary parasite (174). What rôle these organisms play is not known, though there is good reason to believe that they may follow *T. basicola* and thus aid in the later stages of root-rotting. The presence of these fungi actually within root tissue would suggest this. That *T. basicola* alone is capable of producing severe root-rot is well established, but this does not necessarily rule out the possibility that other soil organisms may, under certain conditions, be associated with *T. basicola.* Moreover, this microscopical technique

is well adapted to studying the sequence of fungi involved, as indicated in investigations in infection of strawberry and tobacco seedlings (138). Obviously this technique has its limitations in that it does not follow that all the organisms encountered in roots are necessarily parasites, and certainly microscopic examination alone does not indicate the relative importance of the fungi present. The method has, however, opened up a new approach to the study of root-rots.

In support of the evidence obtained from microscopical studies there is that of inoculation studies to the effect that the parasitic activity of *R. solani* was enhanced when it acted in combination with other fungi associated with the root-rot of cotton in the Punjab, namely *Fusarium solani,* two other strains of *Fusarium* and *Helminthosporium* sp. Also, inoculations made with a mixture of *R. solani* and *R. bataticola* gave increased virulence over inoculations made with either of these fungi alone (322). On the other hand, *R. solani* alone caused a more serious root-rot on *Viola* than when associated with *Pythium* spp. (47), and a mixture of nine strains of *Pythium* was less severe in producing a root-rot of strawberries in Louisiana than any one of the strains alone (237). In another connection, "*Diplodia natalensis* Evans and *Colletotrichum gloeosporioides* Penz. inoculated similarly in slight wounds in citrus bark produced much more marked effects than where each was applied alone" (85), and inoculation of *Phytophthora citrophthora* combined with *Fusarium* sp. produced much more rapidly enlarging lesions of *Pythiacystis* gummosis than did the *Phytophthora* alone (86). The Fusarium when introduced alone was unable to advance at all in this wounded bark.

Another trend, an ecological one, has been the study of the mutual relationship of root-rot organisms to their general soil environment, with special emphasis on the rôle of toxins and antagonistic organisms, and the effects of a changing biological equilibrium on the incidence of root-rot. These studies have established that toxins given off by one organism may affect other organisms adversely by antagonism and that the natural biological equilibrium of a soil may be so changed by manuring, cover cropping, fertilization, rotation, *etc.,* as to render the environment unsuitable for certain specific root-rot-producing parasites, thus reducing the rot. Literature on these phases is rapidly accumulating (33, 34, 130, 132, 133, 197, 219, 264, 268, 285, 336).

The present approach to the study of root-rots, therefore, goes much further than mere host-parasite relationship. Rather, it embraces the inter-association of various components, biological, chemical and physical, as they influence the host-parasite relationship in disease. The limits to our progress in this most complex field are conditioned to-day by our lack of knowledge of much that transpires in a soil, and its relationship to the growing plants; also by lack of suitable technique to study certain phases of the problem, especially the biological and chemical phases.

When it is realized that roots grow in a living, dynamic environment of a most complex nature, it becomes obvious that it is no simple matter to assess correctly the many factors that may be associated in the production of root-rot. Moreover, when it is further realized that any influence which upsets the normal biological balance in the soil, may have a profound effect not only on the soil flora in general, and on the parasites in particular, but on the host plant as well, the difficulties involved in the elucidation of the true nature and cause of certain root-rots become increasingly apparent. Hence, investigations on root-rots, especially of the complex type, should incorporate studies of the chemical, physical and biological interrelationships, in a cooperative investigation, including the chemical, agronomic and biological as well as pathological aspects.

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The Classification of Inflorescences	H. W. RICKETT *New York Botanical Garden*
The Inferior Ovary	GERTRUDE E. DOUGLAS *New York State College for Teachers*
Control of Noxious Plants	H. K. WILSON *University of Minnesota*
Classification of the Green Algae	F. E. FRITSCH *University of London*
Recent Studies on the Inheritance of Size and Shape in Plants	H. H. SMITH *Bureau of Plant Industry*
Radiation and Plant Respiration	R. L. WEINTRAUB *Smithsonian Institution*

Articles arranged for most recently

Nematode Diseases of Plants	A. L. TAYLOR *Bureau of Plant Industry*
Plant Disease Introduction	W. A. MCCUBBIN *Bureau of Entomology and Plant Quarantine*
Control of Fungi in Lumber during Air-Seasoning	A. F. VERRALL

Articles in course of preparation

Endomitosis	A. LORZ *Seton Hall College*
The Male Gametophyte of Angiosperms	A. GERSHOY *University of Vermont*
Techniques for Aseptic Growth of Plants	L. C. KNORR *Cornell University*
The Cytology of Fertilization in Angiosperms	L. E. ANDERSON *Duke University*
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